Evolutionary patterns of range size, abundance and species richness in Amazonian angiosperm trees

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Amazonian tree species vary enormously in their total abundance and range size, while Amazonian tree genera vary greatly in species richness. The drivers of this variation are not well understood. Here, we construct a phylogenetic hypothesis that represents half of Amazonian tree genera in order to contribute to explaining the variation. We find several clear, broad-scale patterns. Firstly, there is significant phylogenetic signal for all three characteristics; closely related genera tend to have similar numbers of species and similar mean range size and abundance. Additionally, the species richness of genera shows a significant, negative relationship with the mean range size and abundance of their constituent species. Our results suggest that phylogenetically correlated intrinsic factors, namely traits of the genera themselves, shape among lineage variation in range size, abundance and species richness. We postulate that tree stature may be one particularly relevant trait. However, other traits may also be relevant, and our study reinforces the need for ambitious compilations of trait data for Amazonian trees. In the meantime, our study shows how large-scale phylogenies can help to elucidate, and contribute to explaining, macroecological and macroevolutionary patterns in hyperdiverse, yet poorly understood regions like the Amazon Basin.

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24   **ABSTRACT**

25   Amazonian tree species vary enormously in their total abundance and range size, while

26   Amazonian tree genera vary greatly in species richness. The drivers of this variation are not well

27   understood. Here, we construct a phylogenetic hypothesis that represents half of Amazonian tree

28   genera in order to contribute to explaining the variation. We find several clear, broad-scale

29   patterns. Firstly, there is significant phylogenetic signal for all three characteristics; closely

30   related genera tend to have similar numbers of species and similar mean range size and

31   abundance. Additionally, the species richness of genera shows a significant, negative relationship

32   with the mean range size and abundance of their constituent species. Our results suggest that

33   phylogenetically correlated intrinsic factors, namely traits of the genera themselves, shape

34   among lineage variation in range size, abundance and species richness. We postulate that tree

35   stature may be one particularly relevant trait. However, other traits may also be relevant, and our

36   study reinforces the need for ambitious compilations of trait data for Amazonian trees. In the

37   meantime, our study shows how large-scale phylogenies can help to elucidate, and contribute to

38   explaining, macroecological and macroevolutionary patterns in hyperdiverse, yet poorly

39   understood regions like the Amazon Basin.

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47   **Introduction**

48   Some Amazonian tree species attain incredibly high abundance (tens to hundreds of millions of

49   mature individuals), while most have small populations sizes, numbering in the thousands to tens

50   of thousands of individuals (ter Steege *et al.* 2013, 2015). Similarly, the range of some

51   Amazonian tree species extends across the entire Amazon basin, while most are restricted to

52   much smaller areas (Kristiansen *et al.* 2009). A similar imbalance is observed in species to genus

53   ratios. Over half of all Amazonian tree species belong to genera with 100 or more species, while

54   the majority of genera (52%) have ten or fewer species (Gentry 1993). The drivers of variation in

55   these fundamental characteristics of tree species and genera are poorly known, despite the

56   Amazon representing the largest tropical forest in the world and housing the greatest number of

57   tree species of any forest (Fine & Ree 2006).

58

59   Variation in the abundance of tree species at the community level is evident in any forest and has

60   been studied in tropical forests since at least 1979 (Hubbell 1979). However, only relatively

61   recently has sufficient taxonomic and forest inventory work been carried out at sufficiently large

62   spatial scales (>1000 km) to explore patterns of dominance across the Amazon; the results have

63   shown conclusively that certain tree species dominate at large spatial scales as well (Pitman *et al.*

64   2001, ter Steege *et al.* 2013, 2015). Neutral ecological models where species drift randomly in

65   abundance over time can generate variation in abundance, but they fail to explain the consistent

66   dominance of some tree species across the Amazon (Hubbell 2001, Condit *et al.* 2002). This

67   begs the question of which characteristics or traits allow certain tree species to dominate, but the

68   absence of adequate trait datasets has limited attempts to answer this question. There are two

69   large-scale databases available that provide reasonable coverage of Amazonian tree species, for

70   wood density and seed mass (Zanne *et al.* 2009, Royal Botanic Gardens Kew 2016), but these

71   two traits do not appear to be related to tree abundance in the Amazon (ter Steege *et al.* 2013,

72   2015). At smaller spatial scales, tree height has been shown to be positively correlated with

73   abundance (Pitman *et al.* 2001, Arellano *et al.* 2014), but it is unclear if this pattern holds at the

74   scale of the entire Amazon Basin.

75

76   There has been less progress in studying variation in the range size of Amazonian trees, in large

77   part because many areas of the Amazon remain poorly known by botanical scientists. In 1999,

78   Pitman and colleagues noted that "not a single tree species distribution in the Amazon basin has

79   been reliably mapped" (Pitman *et al.* 1999), and this remains the case. Nevertheless, with some

80   simplifying assumptions, Feeley and Silman (2009) succeeded in providing a first estimate of the

81   range size of thousands of Amazonian plant species. These authors documented substantial

82   variation in the range size of Amazonian tree species, but, given their focus on conservation, they

83   did not attempt to explain this variation, and neither has any subsequent study. Range size has

84   been shown to be positively related to the total abundance of tree species in the Amazon (ter

85   Steege *et al.* 2013), but the arrow of causality probably goes in the reverse direction (*i.e.* tree

86   species with larger ranges can achieve greater total abundance). Meanwhile, studies of a more

87   limited taxonomic scope have shown that range size in Amazonian palm tree species (Arecaceae)

88   is positively related to their height (Ruokolainen et al. 2002; Kristiansen *et al.* 2009). Whether

89   this pattern holds for dicotyledenous Amazonian trees is unknown, and whether other tree traits

90   are related to range size remains to be explored.

91

92   Lastly, while variation in the species richness of tree genera in the Amazon has been noted (*e.g.*

93   Bermingham & Dick 2001), it has received surprisingly little research attention compared to the

94   extensive efforts directed toward understanding the extraordinary *total* tree species richness of

95   the Amazon (Prance 1982, Hoorn *et al.* 2010). Baker *et al.* (2014) represents a landmark in this

96   regard, as the authors focused on explaining variation in species richness *amongst* 51 Amazonian

97   tree lineages (primarily genera). The authors focused on assessing the role of intrinsic factors

98   (*i.e.* traits of the lineages themselves) as compared to extrinsic factors (*e.g.* geological events) in

99   explaining this variation. They showed that the species richness of genera was negatively related

100   with their turnover time; genera that showed higher mortality and recruitment rates in forest

101   inventory plots also had more species. Meanwhile, they did not find a relationship of species

102   richness with dispersal syndrome, breeding system or tree height. The negative results in this

103   study may be best considered as preliminary however, given that the study covered only 51 tree

104   genera (among 100s in the Amazon) and only trees ≥10 cm diameter at breast height (1.3 m

105   above the ground), which was the minimum size threshold for sampling trees in the forest

106   inventory plots used to estimate turnover times.

107

108   Acquiring sufficient trait data to thoroughly evaluate the drivers of variation in the abundance,

109   range size and species richness of Amazonian tree lineages will require many costly field

110   campaigns that will likely take multiple decades to complete. In the meantime, alternative

111   approaches should be pursued. One fundamental question is whether intrinsic or extrinsic factors

112   are more important. To the degree that intrinsic factors or traits (*e.g.* tree height or dispersal

113   syndrome) show phylogenetic signal (*cf.* Freckleton *et al.* 2002, Blomberg *et al.* 2003), large-

114   scale phylogenies could be used to test the role of intrinsic factors in driving variation in

115 abundance, range size and species richness. In other words, if closely related lineages tend to

116 have similar abundance, range size and species richness, then phylogenetically correlated traits

117 are likely to be important drivers of variation in these characteristics. It is improbable that

118 extrinsic factors would generate phylogenetic signal for abundance, range size or species

119 richness within a given biogeographic region. Recent advances in the generation of sequence

120 data for large numbers of Amazonian tree genera (*e.g.* Baraloto *et al.* 2012) mean that

121 phylogenetic approaches are now feasible. Here, we generate a temporally-calibrated

122 phylogenetic hypothesis that includes half of all Amazonian tree genera. We use this genus-level

123 phylogeny to assess if there is phylogenetic signal for the mean range size, mean abundance and

124 species richness of genera, with the aim of testing the importance of intrinsic traits of genera in

125 driving macroecological and macroevolutionary patterns in Amazonian trees.

126

127 **Methods**

128 We intersected a list of all Neotropical tree genera (from

129 http://ctfs.si.edu/webatlas/neotropicaltree/) with a list of Amazonian plant species (Feeley &

130 Silman 2009) in order to generate a list of Amazonian tree species. The Feeley and Silman

131 (2009) dataset additionally includes estimates of range size for all species. We obtained estimates

132 for the total abundance of Amazonian tree species from ter Steege *et al.* (2013).

133

134 We obtained sequences of the *rbcL* plastid gene for 631 Amazonian angiosperm tree genera

135 (Table S1), with 567 sequences coming from Genbank (www.ncbi.nlm.nih.gov/genbank/) and an

136 additional 64 genera being newly sequenced following protocols outlined in Baraloto *et al.*

137 (2012). We obtained sequences of the *matK* plastid gene from Genbank for 452 of the 631

138 genera with *rbcL* data (Table S1). Sequences were aligned using the MAFFT software (Katoh &

139 Standley 2013). 'Ragged ends' of the sequences that were missing data for most genera were

140 manually deleted from the alignment. Preliminary phylogenetic analyses allowed us to exclude

141 sequences from GenBank for genera that were phylogenetically placed in a different family to

142 that which they are thought to belong taxonomically. The final alignment can be found in the

143 Supplementary Material.

144

145 We estimated a maximum likelihood phylogeny for the genera in RAxML v8.0.0 (Stamatakis,

146 Hoover & Rougemont 2008), on the CIPRES web server (www.phylo.org). We used the default

147 settings, including a General Time Reversible (GTR) + Gamma (G) model of sequence

148 evolution, with separate models for the *rbcL* and *matK* genes (*i.e.* a partitioned analysis). We

149 included sequences of *Amborella trichopoda* (Amborellaceae) and *Nymphaea alba*

150 (Nymphaeaceae) as outgroups. This phylogeny (see Supplementary Material) was used as a

151 starting tree for simultaneous topology and divergence time estimation in the software BEAST

152 v1.82 (Drummond & Rambaut 2007). We implemented fossil-based age constraints for 25 nodes

153 distributed across the phylogeny, using log-normal prior distributions with an offset to impose a

154 hard minimum age (see Table S2). We used a GTR + G model of sequence evolution, with

155 separate models for the *rbcL* and *matK* genes, an uncorrelated relaxed lognormal clock, and a

156 birth-death model for the speciation process. We conducted several preliminary runs to optimise

157 the tuning and weight of parameters as per recommendations generated by the software. Once

158 parameter optimisation stabilised, we ran two separate chains for 100 million generations. The

159 first 50 million generations of each chain were discarded as "burn-in", as the posterior

160 probability of the phylogeny did not stabilise until this point. We combined the post burn-in

161   posterior distributions of parameters and confirmed that effective sample size (ESS) values

162   exceeded 100 for all parameters. We then used the phyutility software (Smith & Dunn 2008) to

163   generate an all-compatible consensus tree from the combined post burn-in posterior distribution

164   of trees. Node ages were optimised onto this consensus phylogeny as the median value for a

165   given node across all trees in the posterior distribution that contained the node (using the

166   TreeAnnotator software, Drummond & Rambaut 2007).

167

168   For each genus in the phylogeny, we calculated the mean range size and abundance for all

169   constituent species in the Feeley and Silman (2009) and ter Steege *et al.* (2013) datasets. Of the

170   631 genera in the phylogeny, 493 had an abundance estimate for at least one species in ter Steege

171   *et al.* (2013). We considered the number of species for each genus in the Feeley and Silman

172   (2009) dataset as an estimate of the species richness of that genus in the Amazon. As an

173   alternative estimate, we used the Neotropical species richness estimates for genera in Gentry

174   (1993), which produced highly similar results. We assessed correlations amongst these genus-

175   level characteristics using Pearson's correlation coefficients for both the raw values and for their

176   phylogenetically independent contrasts.

177

178   We tested for phylogenetic signal for each of these genus-level characteristics using Pagel's λ

179   (Freckleton, Harvey & Pagel 2002). Under Brownian motion evolution, where trait values drift

180   randomly over evolutionary time and where the phylogenetic relationships of taxa perfectly

181   predict the covariance among taxa for trait values, the expected value of λ is one. When the

182   phylogenetic relationships of taxa do not predict the covariance at all, the expected value of λ is

183   zero. We compared the fit of different values for λ (one, zero and the maximum likelihood

184   estimate) using the Akaike information criterion (AIC).

185

186   In order to determine which lineages may be responsible for significant phylogenetic signal for a

187   given characteristic (*e.g.* mean range size of genera), we used the following approach. We first

188   estimated the ancestral value at each node in the phylogeny using maximum likelihood ancestral

189   state reconstruction (Schluter *et al.* 1997). We then randomised the tips of the phylogeny 1000

190   times, reconstructed ancestral values at nodes each time, and compared the observed

191   reconstructed value to that across the randomisations. If the observed value for a node was

192   greater than that in 97.5% of the randomisations, we considered the lineage descending from that

193   node to show significantly high values for the trait, while if the observed value was lower than

194   2.5% of the randomisations, we considered the lineage to show significantly low values.

195

196   In order to assess whether major clades (Magnoliids, Monocots, Rosids and Asterids) differ in

197   the species richness and mean range size and abundance of their constituent genera, we used

198   analyses of variance with major clade as the grouping variable. In order to determine which

199   clades may be driving significant results, we used Tukey's tests. All analyses were conducted,

200   and figures constructed, in the R Statistical Software (R Core Development Team 2016) using

201   functions in the ape (Paradis *et al.* 2016), geiger (Harmon *et al.* 2016) and phytools (Revell

202   2016) packages (see Supplementary Material for codes).

203

204   **Results**

205   The phylogeny derived from the DNA sequence dataset that we compiled spans from the

206   Magnoliids to the Asterids, thus encompassing all major clades of angiosperms (Fig. 1; see

207   Supplementary Material for newick-formatted tree file). The 64 *rbcL* sequences that were

208   generated as part of this study represent ~10% of the genera in the phylogeny, and they therefore

209   represent a valuable contribution to our understanding of the evolutionary relationships of

210   Amazonian tree genera. Most orders and families were monophyletic in the phylogeny with the

211   notable (previously known) exceptions of Olacaceae and Icacinaceae, while the large-scale

212   phylogenetic relationships are largely in agreement with those from recent, angiosperm-wide

213   phylogenetic analyses (*e.g.* Magallón *et al.* 2015).

214

215   The species richness of genera is negatively correlated with mean range size ($r = -0.40$, $p <$

216   0.001) and mean abundance ($r = -0.38$, $p < 0.001$). These relationships are weaker, but still

217   significant, when using phylogenetically independent contrasts (PICs), indicating that

218   phylogenetically related traits partially underlie the correlations (mean range size PICs: $r = -0.28$,

219    $p < 0.001$; mean abundance PICs: $r = -0.24$, $p < 0.001$; Fig. 2). Meanwhile, mean range size and

220   abundance of genera are strongly positively correlated, using both the raw data and PICs ($r =$

221   0.44, $p < 0.001$; PICs: $r = 0.43$, $p < 0.001$). All of the genus-level characteristics show significant

222   phylogenetic signal, but less than would be expected under a Brownian motion model of

223   evolution (Table 1).

224

225   Significant phylogenetic signal for these characteristics is driven by significantly high or low

226   values in many lineages (Fig. 1, Table S3). Diverse lineages in the Magnoliids and the Asterids

227   show high species richness and low mean range size and abundance, including the Lamiales and

228 multiple lineages in the Rubiaceae and Solanales. One marked exception to the general pattern in

229 the Asterids is Lecythidaceae, which shows low species richness and high abundance.

230 Meanwhile, many lineages in the Rosids show low species richness and high mean range size

231 and abundance, including Euphorbiaceae, Salicaceae and Moraceae. Within the Rosids, the

232 exception to this pattern is found in multiple lineages in the Myrtales, including the

233 Melastomataceae, which show a pattern similar to most lineages in the Asterids. The

234 Leguminosae (Fabaceae), the most genus-rich family in our dataset, does not show any

235 significant departures from null expectations, although individual lineages therein show low

236 species richness and high mean range size. Within the monocots, the Arecaceae show low mean

237 range size, while one lineage (*Iriartea* with *Socratea*) shows particularly high abundance.

238

239 A non-phylogenetic comparison of genera in the major clades shows they are not significantly

240 different in terms of mean species richness (ANOVA for species richness: $F = 1.18$, $p = 0.317$),

241 while they are significantly different for mean range size and abundance, but the effect sizes are

242 small (range size: $F = 10.56$, $p < 0.001$, $R^2 = 0.05$; abundance: $F = 7.13$, $p < 0.001$, $R^2 = 0.04$).

243 Tukey's tests reveal that genera in the Rosids have significantly larger mean ranges, on average,

244 than genera in the Asterids ($p < 0.001$) and Monocots ($p = 0.019$), while genera in the Rosids

245 and Monocots have significantly higher mean abundance than genera in the Asterids ($p < 0.001$

246 & $p = 0.020$, respectively).

247

248 **Discussion**

249 Fundamental characteristics of Amazonian tree genera, namely their species richness and the

250 mean range size and abundance of their constituent species, show marked and significant

251   phylogenetic signal (Table 1). In other words, closely related genera tend to have similar

252   numbers of species and species with similar range sizes and abundances (Fig. 1). These genus-

253   level characteristics are also strongly correlated with each other (Fig. 2). Our results suggest that

254   intrinsic factors (*i.e.* traits of the genera themselves) exert a strong influence on the range size,

255   abundance and species richness of Amazonian tree species and genera.

256

257   We propose that tree height may be one of the key traits underlying the observed results. Many

258   of the lineages in our study that show high species richness and small geographic ranges (*e.g.*

259   Myrtaceae, Melastomataceae, Rubiaceae, Asterales, Solanales, and Lamiales) tend to be small in

260   stature. Previous studies have shown a positive relationship between the height of Amazonian

261   trees and their range size (Ruokolainen *et al.* 2002, Kristiansen *et al.* 2009). Such a relationship

262   may be due to larger-statured trees being able to disperse their seeds greater distances, likely

263   through greater fecundity, which would increase the chances that at least some seeds make it a

264   long distance and would, for animal-dispersed species, potentially attract more dispersers.

265   Increased dispersal ability would also increase gene flow among distant populations, which, in

266   turn, could reduce opportunities for allopatric isolation and contribute to reduced diversification.

267   Smaller statured trees may also have shorter generation times, which could contribute to

268   increased diversification (Baker *et al.* 2014). Thus, small-stature may be a biological trait that

269   spurs diversification and may also underlie the negative correlation between mean range size and

270   species richness of genera. Small-statured lineages also show lower abundances in the datasets

271   assembled, although this is partly, if not entirely, explained by the abundance estimates being

272   derived from tree plots that survey individuals >10 cm diameter at breast height (ter Steege *et al.*

273   2013). Meanwhile, the relationship between mean abundance and species richness of genera may

274   simply be a by-product of correlations between range size and abundance. These are likely

275   necessarily related as the range size of a species will restrict the total abundance that it can

276   achieve.

277

278   Our focus on tree height as a key variable does not negate a role for other phylogenetically

279   correlated traits in contributing to the observed results. In local-scale studies of Amazonian tree

280   communities, most of the traits that have been examined (*e.g.* wood density, specific leaf area)

281   have shown significant phylogenetic signal (Kraft & Ackerly 2010, Baraloto *et al.* 2012). Large-

282   scale compilations of trait data from across the Amazon are now needed in order to assess which

283   exact traits may be driving our results.

284

285   It is important to note that the phylogenetic signal we observe for these genus-level

286   characteristics is less than would be expected under a Brownian motion model of evolution. In

287   fact, the Brownian model fits the data much worse than a simple model whereby there is no

288   phylogenetic dependence to the observed values (Table 1). This result may be due to some

289   evolutionary process, such as selection, driving closely related genera to diverge in values for the

290   studied genus-level characteristics. However, in contrast to what might be thought for other traits

291   (*e.g.* those related to ecological niches such as resource acquisition or defence strategy), it is not

292   immediately clear why selection would favour divergence among closely related lineages in their

293   diversification rate, average range size or average abundance. Alternatively, a Brownian motion

294   model may be simply a poor descriptor of how these genus-level characteristics change over

295   time. The Brownian motion model stipulates that per unit time, small changes in trait values are

296   much more likely than large changes. It may be the case that large changes in range size,

297   abundance and diversification rate among closely related changes are just as likely as small

298   changes. The exact pattern of change in these characteristics would depend on how the

299   underlying driving factors themselves, be they intrinsic or extrinsic, change over time and space.

300

301   In any case, the phylogenetic signal we document is evident across multiple phylogenetic scales.

302   At a broad scale, we find that various lineages in the Rosids are comprised of genera that show

303   low species richness and high mean range size and abundance, while lineages in the Magnoliids

304   and Asterids show the opposite pattern. Interestingly, a non-phylogenetic approach, using

305   analyses of variance, did not find large differences amongst these major lineages. This contrast in

306   results may be due in part to lineages within the major clades that belie the general pattern. For

307   example, the Myrtales (in the Rosids) show a pattern typical of the Asterids, while the

308   Lecythidaceae (in the Asterids) show a pattern typical of Rosids. The contrast is likely also due

309   to the manner in which these genus-level characteristics are distributed across the phylogeny.

310   While genera within a given major clade can show a diversity of values for these characteristics,

311   their relative phylogenetic positions result in reconstructed ancestral values that show systematic

312   differences amongst lineages in different major clades. A phylogenetic approach was thus

313   necessary to reveal how these major clades differ have differed over evolutionary time. This

314   phylogenetic approach has also served to show how phylogenetically-correlated factors, intrinsic

315   to lineages themselves, have contributed to the macroecological and macroevolutionary patterns

316   observed in present-day Amazonian trees.

317

318   **Acknowledgements**

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453 **Data accessibility**

454   DNA sequences: For Genbank accession numbers, see Table S1.

455   Phylogeny: TreeBASE, http://purl.org/phylo/treebase/phylows/study/TB2:S19277?x-access-

456   code=38f1545d97977839af2bf6a9498817a7&format=html

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476   **Table 1**: ΔAIC values for different evolutionary models of trait evolution for genus-level

477   characteristics and for different values of Pagel's λ.

Genus characteristic	Evolutionary Model	λ	ΔAIC
log (Species richness)	estimated λ	0.26	0
	no phylogenetic dependence	0	-17.1
	Brownian motion	1	-287.8
log (Mean range size)	estimated λ	0.37	0
	no phylogenetic dependence	0	-52.0
	Brownian motion	1	-257.9
log (Mean abundance)	estimated λ	0.32	0
	no phylogenetic dependence	0	-34.2
	Brownian motion	1	-287.5

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488   **Figure 1:** Phylogeny of 631 Amazonian tree genera with terminal branches coloured according

489   to the **(A)** species richness, **(B)** mean range size, and **(C)** mean abundance of genera. The

490   following numbered nodes are mentioned in the main text: 1=Arecaceae, 2=Magnoliids,

491   3=Rosids, 4=Asterids, 5=Myrtales, 6=Melastomataceae, 7=Euphorbiaceae, 8=Salicaceae,

492   9=Moraceae, 10=Leguminosae, 11=Lamiales, 12=Rubiaceae, 13=Solanales, and

493   14=Lecythidaceae. Nodes that are coloured blue indicate lineages whose constituent genera show

494   significantly higher values for the given genus-level characteristic than expected by chance,

495   while nodes coloured red show significantly lower values than expected by chance.

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497   **Figure 2:** Relationships between species richness and mean range size and abundance for

498   Amazonian tree genera. Histograms of each genus-level characteristic are given on the diagonal.

499   Below the diagonal the raw relationships are shown along with the best-fit linear relationship and

500   the Pearson correlation coefficient. Above the diagonal, the relationships of phylogenetically

501   independent contrasts (PICs) are shown along with the best-fit linear relationship that is forced

502   through the origin and the Pearson correlation coefficient.

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511 **Figure 1**
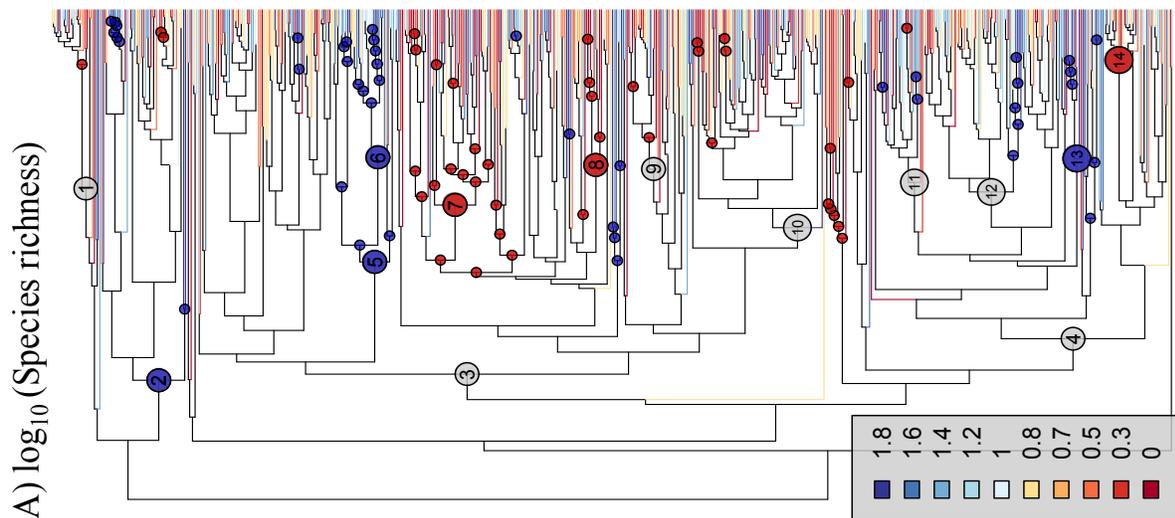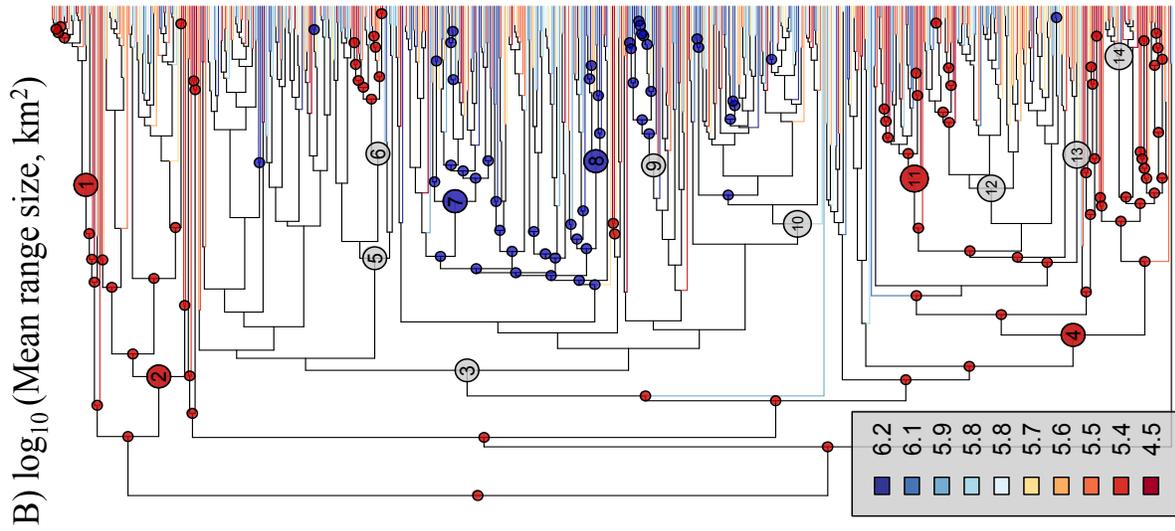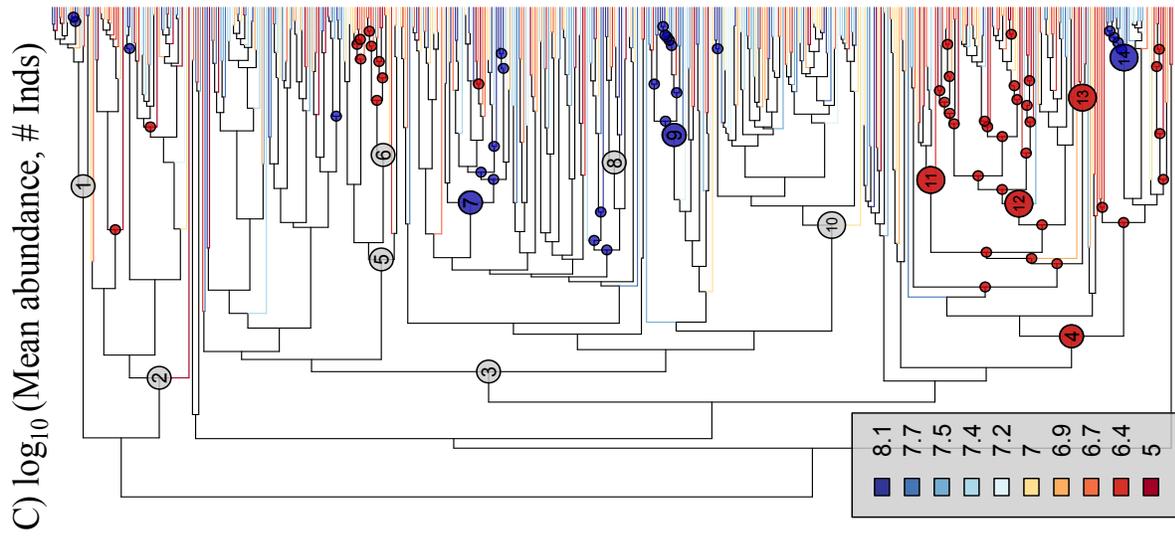
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513   **Figure 2**
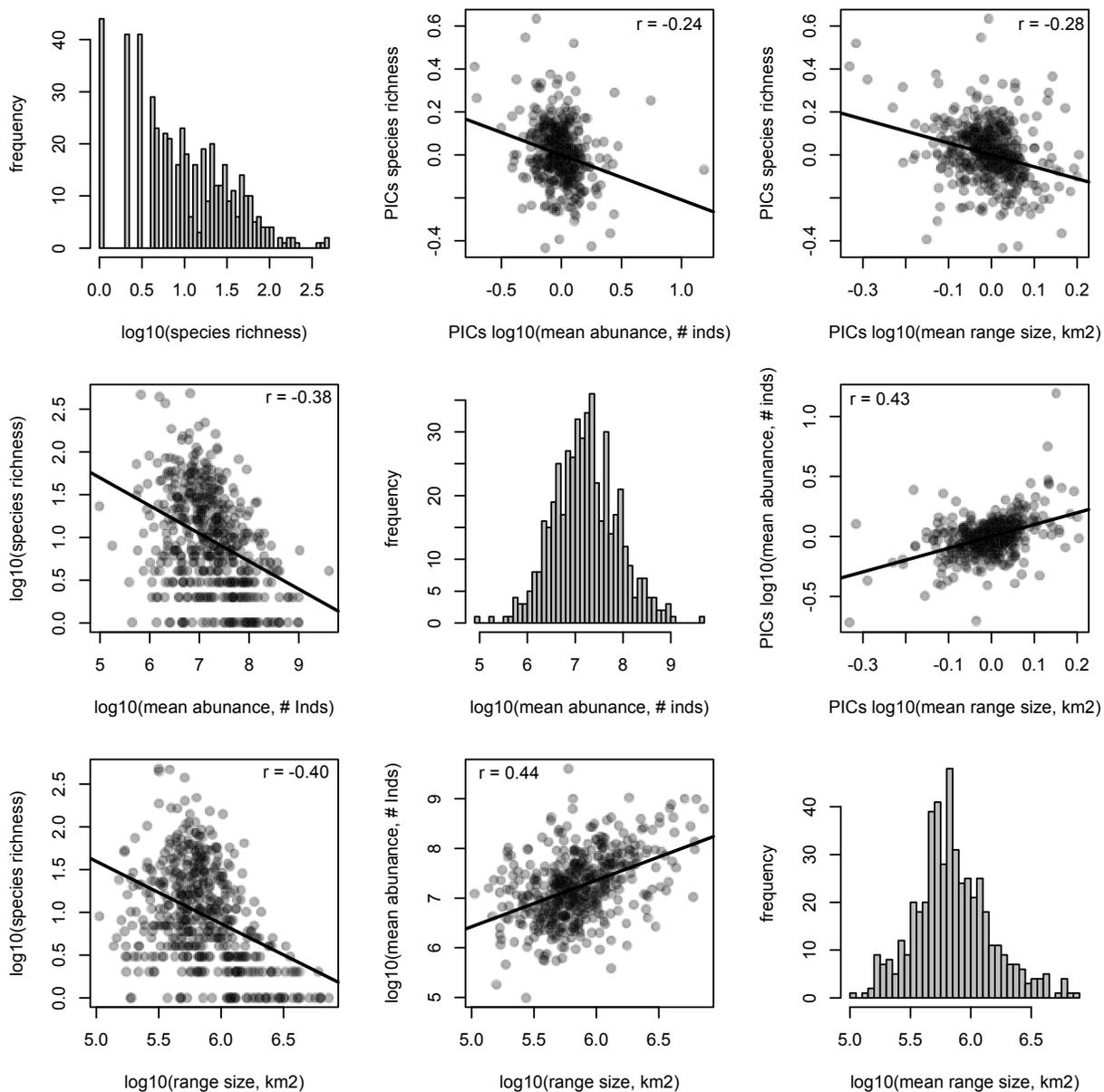
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520 **Supplementary Files**

521 **Table S1:** Amazonian tree genera in the phylogeny generated in this study, along with the

522 species to which each rbcL and matK accession belongs and the associated Genbank accession

523 numbers. For novel sequences, we also give the collection number.

524 **Table S2:** Nodes in the phylogeny that were constrained based on fossil ages in the temporally-

525 calibrated phylogenetic analysis. The hard minimum age allowed for the node (*i.e.* the offset)

526 and the mean and standard deviation of the log-normal prior are given, in millions of years.

527 **Table S3:** Taxonomic lineages present in the phylogeny along with their reconstructed values for

528 species richness, range size and abundance (all log transformed to the base 10 prior to analysis).

529 The probability that a given lineage has a smaller value than that reconstructed is also given,

530 based on a permutation test described in the main text. If this probability is smaller than 0.025,

531 then the lineage is described as having a significantly smaller value than expected by chance,

532 while the converse holds if the value is greater than 0.975.

533 **rbcL_matK_alignment.fasta:** Final sequence alignment used in phylogenetic analyses. The two

534 genes are concatenated, with rbcL forming the first 1320 base pairs of the alignment.

535 **Amazon_genus_phylog_RAxML.tre:** Maximum likelihood phylogeny for Amazonian tree

536 genera.

537 **Amazon_genus_phylog_BEAST.tre:** Temporally-calibrated phylogeny for Amazonian tree

538 genera. This is the all-compatible consensus tree generated from the posterior distribution of

539 trees from a Bayesian phylogenetic analysis, with node ages representing the median value for

540 each node across the posterior distribution of trees.

541 **Dexter_AmazonTrees_script.R:** The script for all analyses conducted for this manuscript in the

542 R Statistical Software.

543   **taxonomy_table.csv:** Infile used in the R script, which contains the taxonomic classification for

544   each genus in the study.